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SHORT COMMUNICATION

Courtship behaviour of manakins and seed bank composition in a French Guianan rain forest

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The size and species composition of both the seed rain and the seed bank at a forest site are important factors determining future regeneration (De Foresta & Prévost 1984, Garwood 1989, Putz & Apannah 1987). Seed dispersers can influence the regeneration potential of (tropical) forests by means of the seed rain they generate (Garwood 1989, Janzen 1983). In this study, we present an example of how the courtship behaviour of an avian frugivore of the manakin family (Passeriformes, Pipridae) can induce both seed clumping and modification of the species composition in the seed bank at specific forest sites.

Manakins are small frugivorous birds and most species have a lek mating system where males aggregate into groups to display with each male defending its own small territory. In the breeding season, typically lasting about 6 mo a year, males spend up to 90% of their time on and around their lek where they sing from perches and perform display dances to attract females to mate with (Snow 1962a, Théry 1992). Adult males only leave their perches for short feeding bouts lasting 2–5 min on nearby fruiting trees (Théry 1990a). Because ingested seeds are defecated or regurgitated after 12–18 min (Worthington 1989, Théry 1990a), we hypothesize that almost all seeds consumed by lekking male manakins are deposited on their leks. In the reproductive season, fruits

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of the Melastomataceae family have been demonstrated to make up a large proportion of the diet of several species of manakins (see below) so their seeds can be expected to be over-represented in the seed rain at leks of these species. Melastomes have specific germination requirements that are strongly dependent on gap-related environmental conditions such as the availability of light and the presence of root mounds (Ellison *et al.* 1993, Putz 1983). At least in French Guiana, manakin leks are not situated in gaps (Théry 1990a) and hence melastome seeds deposited at leks can be expected to accumulate in the seed bank where they stay dormant for an unknown period.

The aim of this study was to test the predicted increased seed density and Melastomataceae-biased floristic composition of the seed bank at manakin leks.

To test this hypothesis we compared the number of seedlings emerging from soil samples taken at respectively leks of two species of manakins, and in the surrounding forest. The study was carried out from July–October 1993 at the Nouragues Biological Station in undisturbed evergreen rain forest 100 km south of Cayenne in French Guiana (4°5′N, 52°40′W). We studied the seed bank of leks of two manakin species: *Corapipo gutturalis* (L.) and *Manacus manacus* (L.). Leks of *C. gutturalis* consist of five to eight males, each male displaying on its own mossy log under closed canopy (Théry 1990b, 1992). Display logs are dispersed over a relatively large area ('exploded' type lek). Males spend most of their time singing from several perches (1–10 m above the ground) near their logs (Théry 1990b). Studied leks of *M. manacus* were situated on the slope of an inselberg covered by open savanna-bush vegetation consisting of dispersed *Clusia* spp. bushes on granitic outcrop. Their lek mating system is of the classical or true type (Bradbury 1981): males aggregate in a small area defending their individual display sites. *M. manacus* leks measure 15–20 m in diameter and are formed by four to thirteen males (Théry 1992).

At five *C. gutturalis* display sites, two pairs of soil samples were taken: one pair near the display log (under one of the perches) and one pair in similar vegetation in the surrounding forest at a distance of 50 m from the display log (control). Because of the patchiness of the vegetation in which leks of *M. manacus* are situated a different sampling strategy was adopted here. At two leks (lek A and B) soil samples were taken on three locations: at the lek site, and at two locations (controls) in the surrounding vegetation. The controls were situated in vegetation similar to the lek (open savannah-bush vegetation) and at equal distance from the mature high forest border and at random distance from the lek. At the lek site, soil samples were taken at randomly-selected locations close to the display territories: 11 at lek A and six at lek B. At each of the control locations, five soil samples were taken randomly. The soil samples were taken using a cylindrical core and measured 0.13 $m^2 \times 3$ cm. In order to reduce the volume, the samples were successively washed through two sieves with decreasing mesh-sizes (the smallest was 0.25 mm). Seeds of Melastomataceae are small to minute (Roosmalen 1985). An unknown portion of the smallest seeds may have passed through the sieve, but the treatments were the same for both lek and control samples. The residue in the last sieve was split into eight equal parts, one of which was spread out on a layer of sterilized sand in a plastic box. The germination boxes were protected from seed immigration by a transparent cover. All boxes were placed in the centre of a large clearing to induce germination under gap conditions. The samples were kept moist by regularly spraying them with water. Germinations were counted at regular intervals for 4 mo. Seedlings were classified into morphospecies which were classified into Melastomataceae, non-Melastomataceae or unidentified in the field laboratory.

To examine differences in seed density between lek and control samples in *C. gutturalis* samples, the numbers of seedlings emerging from each pair of soil samples were averaged, resulting in two estimations of seed density per display log: one for display site samples and one for controls. For the *M. manacus* samples, the numbers of emerged seedlings were averaged per sample group (lek, controls 1 and 2). The count data on seed density were square root transformed (sqrt[x + 1]), and portions of melastome species derived from the seed density data had the angular transformation (arcsine(sqrt[x])).

From both lek and control samples of *C. gutturalis* leks the first seedlings emerged after 17 to 19 d of exposure to full daylight. The emergence of new seedlings continued until the experiment was ended after 4 mo of exposure. Both the total viable seed density and the melastome viable seed density were higher in lek samples than in control samples (Figure 1; paired t-test: $t = 9.14$, $P < 0.001$ and $t = 4.49$, $P < 0.05$, respectively; for both $df = 4$). Also the proportion of viable melastome seeds in the lek samples was higher than in control samples (paired t-test: $t = 3.63$, $df = 4$, $P < 0.05$), indicating that melastomes are disproportionally represented in the seed bank at the display sites.

In the *M. manacus* experiment, the first seedlings emerged after 9 to 13 d and new seeds germinated until the experiment was stopped (after 4 mo of exposure). No significant differences in total viable seed density were found

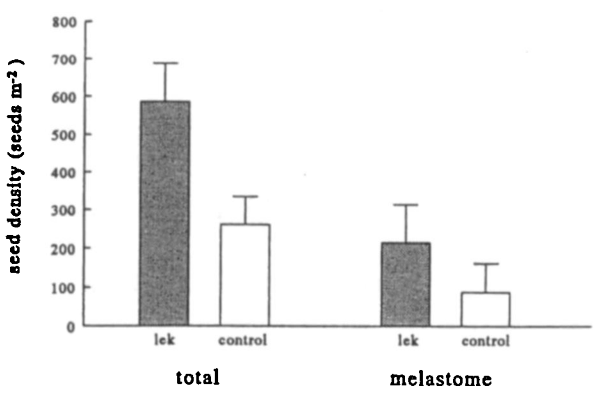

Figure 1. Total seed density and Melastomataceae seed density (mean ± SE) of two group of soil samples, taken at respectively display sites of *C. gutturalis* (lek) and randomly chosen sites in the surrounding forest (control) (n = 5 for both groups).

between lek and control sample groups (one-way ANOVA: df = 20 for lek A, df = 15 for lek B). Although a higher viable melastome seed density was found in one of the control locations (Lek A: one-way ANOVA: F = 3.49, df = 20, $P<0.05$) no significant differences in portion melastome seeds between sample and control samples were found.

Thus, the predicted increase of the overall seed density and over-representation of Melastomataceae seeds in manakin lek soil was confirmed for five sites on leks of *C. gutturalis* but no such trend was found on the two *M. manacus* lek sites. Although clearly more leks of *M. manacus* need to be sampled in order to be conclusive, the observed difference in results for the two species is remarkable considering the much higher density of manakins on leks of *M. manacus* than on *C. gutturalis*. The differences in results could be caused by both differences in (micro) habitat at the studied leks of *M. manacus* and *C. gutturalis* and differences in the dispersal behaviour of the two species. Unfortunately, our data do not allow us to distinguish between these alternatives. Because the soil seed bank and its species composition can be an important factor in the first stages of forest regeneration, the manifestation of higher viable seed density and modified species composition at leks of *C. gutturalis* are expected to influence regeneration potential at these sites. More seeds could germinate in case of gap formation while the species composition of emerging seedlings would be shifted towards the Melastomataceae family.

The strong ecological relationship between manakins and Melastomataceae is often used as a clear example of plant-frugivore mutualism (Charles-Dominique 1993, Snow 1993, Stiles & Rosselli 1966). Indeed, the quantitative measurements of interdependence that we found in the literature show that Melastomataceae fruits make up a substantial proportion of the manakins diet (Table 1). A study by Théry (1990a) showed that diurnal fruit removal by manakins in primary and secondary forests in French Guiana for 20 melastome species ranged from 61–89% (mean 74.1%). Hence, the Melastomataceae seed shadow is likely to be affected by manakin male activity patterns which are concentrated at and around leks (Théry 1992). However, the microclimatic (light) requirements for germination of Melastomataceae seeds are not met at leks of both *C. gutturalis* and *M. manacus*. In a preliminary experiment in which the germination capacity of *C. gutturalis* lek soil under gap and lek conditions was examined, seedlings emerged under gap conditions, but none emerged under lek conditions (Krijger & Opdam 1995). In addition, measurements of canopy opening (using LICOR LAI-2000) demonstrated that light quantity at leks of *C. gutturalis* and *M. manacus* is only a fraction of light quantity in small gaps (Krijger & Opdam 1995). This suggests that the seed shadow produced by lekking manakin males is, in itself, disadvantageous for Melastomataceae fitness. On the other hand, the larger portion of the Melastomataceae fruits is consumed by females and subadult males whose activity pattern is far less concentrated around leks and who spend more time in gaps and gap borders (Théry 1990a). Clearly, there is a need for more quantitative studies in order to assess the actual mutual benefits in this relationship.

Table 1. Contribution of Melastomataceae to the diet of manakins in neotropical wet forests. Importance in diets in percentages (m = male, f = female)

French Guiana[a]:			Costa Rica[b]:	
Pipra pipra	m	58	Manakins	57.8[1]
	f	49		80[2]
P. erythrocephala	m	72		
	f	60	Costa Rica[c]:	
P. serena	m	70		
	f	59	*Pipra mentalis*	44 (n = 41)
Corapipo gutturalis	m	66	*Corapipo leucorrhoa*	28 (n = 18)
	f	54		
Manacus manacus	m	65	Trinidad[d]:	
	f	57		
Tyranneutes virescens	m	71	*Pipra erythrocephala*	63 (n = 455)
	f	60	*Manacus manacus*	47 (n unknown)
Schiffornis turdinus	m	28		
	f	25	Brazil[e]	
			Antilophia galeata	33 (n = 70)

a. From: Théry (1990a). Percentage Melastomataceae seeds in diet, calculated from fecal samples (n = 427) and direct observations of 47 plant species (20 Melastomataceae) at Piste de St. Elie and Nouragues, French Guiana. Values are based on year-round data.
b. From: Stiles & Rosselli (1993). Melastomataceae in fecal samples (n = 302) of manakins caught in mistnets (year-round) at El Plastico, Costa Rica. Percentages are corrected for fecal sample size. [1] Percentage Melastomataceae seeds in diet; [2] percentage of samples containing Melastomataceae seeds.
c. From: Levey (1990). Presence of *one* common species of Melastomataceae (*Miconia centrodesmata*) in fecal samples of two manakin species caught in mistnets in the period of maximal fruiting of *M. centrodesmata* at La Selva (lower montane transition forest), Costa Rica.
d. From: Snow (1962a,b). Percentage Melastomataceae in records of two species of manakins feeding on fruiting plants collected year-round at Simla, Trinidad.
e. From: Marini (1992). Percentage Melastomataceae in the number of plant species visited during foraging at Córrego Capetinga (gallery forest), cerrado region of Brazil.

This study has shown how the presence of a frugivorous bird's lek can influence the seed bank with respect to both seed density and species composition. *C. gutturalis* leks only make up a very small portion of the total forest area, but similar effects can be expected for other primary forest manakin species which together make up a large portion of the forest understorey bird community (Karr *et al.* 1990, Thiollay 1994). In addition, several other frugivorous birds have lek mating systems in which aggregation of dispersed seeds can be expected (Théry & Larpin 1993). This study justifies further research to the extent in which social behaviour of dispersal agents explains variation in regeneration potential on forest level.

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